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How will the semi-natural vegetation of the UK have changed by 2030 given likely changes in nitrogen deposition?

Carly J. Stevens , Richard J. Payne, Adam Kimberley, Simon M. Smart

Abstract

Nitrogen deposition is known to have major impacts on contemporary ecosystems but few studies have addressed how these impacts will develop over coming decades. We consider likely changes to British semi-natural vegetation up to the year 2030 both qualitatively, based on knowledge of species responses from experimental and gradient studies, and quantitatively, based on modelling of species relationships in national monitoring data. We used historical N deposition trends and national predictions of changing deposition to calculate cumulative deposition from 1900 to 2030. Data from the Countryside Survey (1978, 1990 and 1998) was used to parameterise models relating cumulative N deposition to Ellenberg N which were then applied to expected future deposition trends. Changes to habitat suitability for key species of grassland, heathland and bog, and broadleaved woodland to 2030 were predicted using the MultiMOVE model. In UK woodlands by 2030 there is likely to be reduced occurrence of lichens, increased grass cover and a shift towards more nitrophilic vascular plant species. In grasslands we expect changing species composition with reduced occurrence of terricolous lichens and, at least in acid grasslands, reduced species richness. In heaths and bogs we project overall reductions in species richness with decreased occurrence of terricolous lichens and some bryophytes, reduced cover of dwarf shrubs and small increases in grasses. Our study clearly suggests that changes in vegetation due to nitrogen deposition are likely to continue through coming decades.

Keywords

Atmospheric nitrogen deposition; Ellenberg N; Grassland; Heathland; Woodland

1. Introduction

Human activity increasingly dominates the global nitrogen (N) cycle with anthropogenic production of reduced and oxidised N compounds ('reactive N') more than double natural N fixation (Sutton et al., 2011). Although human impact on the global N cycle has a long history, encompassing legume cultivation for several millennia, fossil fuel burning for several centuries and nitrate mining since the 19th century, the critical change was the invention of the Haber-Bosch process (Galloway and Cowling, 2002 and Kopáček and Posch, 2011). Fritz Haber's discovery led to the production of reactive N from inert N₂ on an industrial scale in the post-war era. Global average N deposition increased by more than fourfold from 1860 to 1993 and under an IPCC A2 scenario is predicted to double again by 2050 (Dentener et al., 2006). This increasing deposition will affect an ever greater proportion of the earth's sensitive ecosystems (Bleeker et al., 2011 and Phoenix et al., 2006).

In the United Kingdom oxidised N emissions increased sharply from the 1940s with the greatest increase to 1960 and then a slower increase to a peak around 1980. Reduced N emissions increased more gradually over the same period with total N deposition peaking around 1990 at 430 kt N (Fowler et al., 2004). In recent decades there has been a reduction in emissions of both reduced (–24%; 1990–2007) and oxidised N (–46%; 1990–2007 (RoTAP, 2012)) due to technological change and decline in industrial production. However, changes in atmospheric chemistry have meant that

these reduced emissions have not translated to equivalent declines in deposition, with only minor change in total N deposition over the last 20 years (RoTAP, 2012). N deposition is expected to fall during the current decade due to a decline in vehicle emissions and increased uptake of mitigation measures for agricultural emissions, although only limited further change is predicted by 2030 (RoTAP, 2012).

1.1. Approaches to predicting vegetation change

Although numerous studies have investigated N deposition impacts in contemporary ecosystems, and several have addressed future deposition trends, there has been comparatively little attention to predicting future change across semi-natural habitats. Some work of this type has been conducted as part of the CCE critical loads process. Hettelingh et al. (2008) have applied dose–response functions, based on European N-addition experiments of over two-year duration (Bobbink, 2008 and Bobbink and Hettelingh, 2011), to predict responses of species richness of selected habitats to projected future N deposition. Results suggest modest increases in plant species richness by 2020 in shrubs, forests and grasslands under scenarios of both maximum feasible reduction and current legislation. There are a number of important limitations to this approach, which mean that the tentative results these authors present may not be realistic. The analysis is based solely on experimental studies with the well-known limitations of small spatial scale, short duration, unrealistic treatment regimes, high N loads and high ambient deposition and for many habitats the number of published studies is very limited. Furthermore, by using relationships with current N deposition, models assume instant recovery from reduced deposition, which is not ecologically realistic as N may accumulate and there may be lags in species responses. In relatively-small treated plots surrounded by unaffected vegetation local sources of propagules may allow re-establishment of sensitive species much quicker than in an entire polluted landscape. It is therefore probable that recovery rates may be systematically over-estimated in experimental studies.

An alternative approach to these simple dose–response calculations has been the use of dynamic soil-vegetation model chains combining models such as ForSAFE-VEG, MAGIC, NTM, MOVE and GBMOVE (de Vries et al., 2010, Smart et al., 2010, Sverdrup et al., 2007 and Wamelink et al., 2009). In these approaches a dynamic soil model predicts change in the soil environment in response to changing deposition which feeds into a statistical or process-based model of vegetation response to changing soil conditions. Much of the application of such model chains for prediction has so-far been exploratory but results suggest that, for instance, the biodiversity of Dutch forests will remain constant over the coming decades while that of heathland and grassland will increase (Wamelink et al., 2009). The challenges in such modelling remain considerable due to both the intrinsic complexity of the problem and the limited availability of suitable data sources, in particular paired soil chemistry and vegetation datasets. Results necessarily incorporate large uncertainties. Other predictive studies have modelled just a few dominant plant species (Bobbink and Heil, 1993 and Terry et al., 2004) or focussed on other response variables such as total biomass or biogeochemical function (Aber et al., 1997).

In many terrestrial ecosystems there is evidence that N inputs are considerably greater than N losses to water courses and the atmosphere, with N accumulating in soils over time (Fowler et al., 2004 and Pilkington et al., 2005). Consequently air pollution impact studies have increasingly considered that total cumulative deposition over an extended period of time is a more useful metric than annual

deposition (De Schrijver et al., 2011, Duprè et al., 2010, Phoenix et al., 2012 and Payne, 2014). As current N deposition will never fall to zero, cumulative nitrogen deposition values can only increase. If cumulative N deposition is used as the sole environmental driver in a predictive study an assumption is thereby made that ecosystem recovery from deposition impacts is not possible. If deposition falls, the rate at which deleterious impacts develop may slow but never stop or reverse.

The available experimental evidence suggests that this is a simplification; some recovery in vegetation does occur but total recovery is likely to take an extremely long time, if this is indeed possible. Recovery speed is also likely to vary between habitats depending on the ability of the soils to accumulate N and the vegetation composition. For example, in boreal forests Strengbom et al. (2001) showed no detectable recovery after nine years of N treatment cessation and impacts on vegetation composition were still marked after 47 years of recovery. In hay-meadows several studies have shown impacts lasting more than a decade with no complete return to prior conditions (Kráľovec et al., 2009, Olff and Bakker, 1991 and Stevens et al., 2012a). In UK heathlands experiments have shown impacts on lichen cover, *Calluna vulgaris* growth and flowering and litter nutrients over seven and eight years after N treatment stopped (Edmondson et al., 2013 and Power et al., 2006). Stevens et al. (2012a) suggest that some impacts on vegetation may be non-reversible with less-competitive species unable to replace N-tolerant dominants once established. Indeed where eutrophication and acidification have driven coupled above and below-ground regime shifts in pH, phosphorus availability and nutrient cycling then recovery is highly unlikely to occur by simply reducing deposition (Baer and Blair, 2008, Chen et al., 2013 and Tateno and Chapin, 1997).

Given the scarcity of recovery studies and their limitations we do not consider the realistic incorporation of ecosystem recovery rates to be feasible. Alternatives are either to use current deposition (assuming instant recovery from reduced deposition) or cumulative deposition (assuming no recovery from reduced deposition) as environmental driver. Although neither gives the full picture we believe that the assumption of 'no recovery' is closer to the available experimental results.

Our aim here is to provide provisional predictions of future change in the community composition of UK semi-natural habitats due to N deposition. To do this we assess how possible trends in N deposition may impact on vegetation both qualitatively, on the basis of N addition experiments and gradient studies, and quantitatively by modelling cumulative N deposition relationships with Ellenberg N scores and then using the MultiMOVE model to assess changing species habitat suitability under projected N deposition for the years 2020 and 2030. Overall we hypothesise that over time habitat suitability for many desirable species will decline in all three habitats as a consequence of elevated N deposition resulting in changes in species composition.

2. Methods

Three groups of semi-natural vegetation were considered: grasslands, heaths and bogs, and broadleaved woodlands. Data were taken from the Countryside Survey (CS) of Great Britain (<http://www.countrysidesurvey.org.uk/>) for the years 1978, 1990 and 1998. In CS samples are collected from stratified, randomly selected 1 × 1 km squares, 569 squares were surveyed in the 1998 survey. 2 × 2 m vegetation plots were located within each 1 × 1 km square using a restricted

randomization procedure to reduce aggregation. In each plot all vascular plants and a selected range of the more easily identifiable bryophytes and macrolichens were identified to a species level and cover estimates made to the nearest 5%. The methods used for vegetation monitoring are described in detail in Smart et al. (2003). Plots were only included in the analysis where the vegetation sampled at time 1 could be classified into one of these three major categories of vegetation responsive to nitrogen addition. The assignment of each plot to each category was done on the basis of its species compositional similarity to the habitat types used for the definition of empirical critical loads for nitrogen in Europe. This step was carried out by determining the match between the Countryside Vegetation System class to which each plot was allocated (see Bunce et al., 1999, Smart et al., 2003 and Smart et al., 2004) and the EUNIS codes for ecosystems listed in Achermann and Bobbink (2003). Plots that saw dramatic vegetation change consistent with conifer planting or conversion to grass-ley and arable were excluded from the analysis. Thus the semi-natural grassland category included calcareous, unimproved neutral and acid grasslands. Broadleaved woodlands included all non-conifer dominated woodland plots. Heaths and Bogs included all inland and coastal, dry and wet heaths and mires. Soligenous mire assemblages dominated by sedges and tall herbs were excluded since there were too few plots for analysis.

Nitrogen deposition for the present day and the recent past was quantified using the Centre for Ecology and Hydrology's C-BED model (Smith et al., 2000). N deposition through the 20th Century is based on hind-casting of 1998 C-BED results following Fowler et al. (2004). This hind-casting does not take account of changing spatial patterns due to changing emission sources and, in particular, is likely to over-estimate deposition in remote regions and under-estimate deposition down-wind of conurbations earlier in the twentieth century (Fowler et al., 2004). Projections of N deposition for 2020 and 2030 are based on UK Department of Environment, Food and Rural Affairs predicted trends in industrial and agricultural emissions using the FRAME model which is calibrated to give results equivalent to C-BED (Dore et al., 2007 and Fournier et al., 2004). Both FRAME and C-BED use a 5×5 km grid which was aggregated to a 10×10 km grid by averaging adjacent cells to match CS data. Cumulative deposition for target years was calculated by summing annual data assuming linear trends between model years with a start point at 1900 to encompass the era of greatest anthropogenic N fixation.

The habitat suitability (HS) for individual species was modelled using MultiMOVE (Butler and Smart, 2009 and Smart et al., 2010). MultiMOVE is a small ensemble of plant species niche models that predict the suitability of conditions for a plant species under a particular environmental conditions. The resulting habitat suitability metric ranges between 0 and 1. A correction for differences in the prevalence of each species in the training datasets used to build MultiMOVE was applied (Albert and Thuiller, 2008). This correction ensures that HS values can be compared across species. Ellenberg N scores (Ellenberg, 1974 and Hill et al., 1999) were used as the explanatory variable that is input to MultiMOVE. Mean Ellenberg N scores for a sample plot convey the ecological impact of increased N deposition on the vegetation. Although this is not a direct response to N deposition and does not include impacts of acidification it provides the best available proxy because it integrates across the range of impacts of N on soil and vegetation dynamics. We extracted vegetation quadrat data and unweighted mean Ellenberg N scores for CS plots in grasslands, heaths & bogs and broadleaved woodlands. A model of the relationship between mean Ellenberg N, as the response variable, and

year of each CS and type of habitat, as explanatory variables was derived in using lmer (lme4 R package). The best fitting model was identified using likelihood ratio tests to compare models. The best model was then coded and fitted as a Bayesian mixed model in OpenBUGS (<http://www.openbugs.net/w/FrontPage>). Estimates of future values of mean Ellenberg N were generated by drawing from the posterior distribution of Ellenberg N values within each 1 km square but with the year term set to 2020 and 2030 (Gelman and Hill, 2007). The best model included the main effects of cumulative N deposition, year of survey and habitat group. There was a clear relationship between observed mean Ellenberg N scores and prediction Ellenberg N scores in 1978, 1990 and 1998 (Fig. 1). However, the predictions do not reflect the uncertainty conveyed by the full posterior distributions of each value. Over-fitting is to some extent a consequence of the between-square residual variation being absorbed by the random intercepts fitted for each 1 km square. However, since these 1 km squares are a representative stratified random sample of GB we derive projections of the change in mean Ellenberg N within random locations within each 1 km square. Thus the precision of these predictions is improved as a result of conditioning on the within and between 1 km square variance estimated from the observations from CS for 1978, 1990 and 1998.

The projected mean Ellenberg N scores were then input into MultiMOVE to derive estimated impacts on habitat suitability for each individual species. MultiMOVE uses three methods and a model averaging approach to fit the relationship between species presence or absence and environmental factors. The methods used are generalised linear models, generalised additive models and multivariate adaptive regression splines. Initially the MultiMOVE model was run using CS data from 1998. Predicted changes in Ellenberg N for the years 2020 and 2030 were then used to rerun the MultiMOVE model. All other environmental factors were kept constant. Changes in HS for individual species that occurred in sufficient squares to provide adequate data for analysis and for each of the communities were calculated. To assess changes in HS and account for different levels of change under high and low deposition we divided cells based on whether they were greater than or less than the median cumulative N point which was 1817.6 kg N ha⁻¹.

3. Results and discussion

3.1. Grasslands

In grasslands results of this investigation show average Ellenberg N scores increasing to a small extent between 1998 and 2020 and 2030 (Fig. 2) and species average HS is set to decline by 2030. At high levels of N deposition some species see more than 20% reductions in HS. In grasslands there were 50 species with sufficient data to examine change in HS at both high and low levels of N deposition. Of these, 40 species showed a reduction in HS at high deposition in 2020. Species that showed the greatest negative change in HS were *Carex panicea* (−0.234), *Calluna vulgaris* (−0.190), *Lotus corniculatus* (−0.172) and *Plantago lanceolata* (−0.164) (Fig. 4).

Species that showed the greatest positive change in HS were *Urtica dioica* (−0.061), *Stellaria media* (−0.046) and *Holcus lanatus* (0.039). Six out of the nine species showing positive responses were graminoids. Overall the magnitude of changes in HS were lower for positively responding species than those that responded negatively (Supplementary Table 1). All of the positively responding species are known to be nitrophilic (Hill et al., 1999).

Semi-natural grasslands on acidic substrates have received considerable research attention in recent years. Using the gradient of ambient N deposition in the UK Stevens et al. (2004) showed a clear negative relationship between N deposition and plant species richness. This relationship was examined across the Atlantic biogeographic zone of Europe and a negative relationship was also apparent (Stevens et al., 2010). A number of species were identified as responding negatively to N deposition including *Hypericum pulchrum*, *Plantago lanceolata*, *Hylocomium splendens*, *Achillea millefolium* and *Succisa pratensis* (Payne et al., 2013). Using historical botanical data Duprè et al. (2010) examined the relationship between cumulative N deposition and species richness in acid grasslands and found a negative relationship between N deposition and vascular plant species richness in the UK, Netherlands and Germany. Nevertheless, long-term N addition experiments in UK acid grasslands have failed to show declines in species richness (Phoenix et al., 2012), possibly due to the time required for species to be lost from an individual plot or because, in small plots, rarer species have already been lost or their dynamics go undetected. Changes in species composition and declines in the abundance of some species have been observed (e.g. Carroll et al., 2003). In calcareous grasslands the results from gradient studies for changes in species richness are less clear. Bennie et al. (2006) found a decline in species richness in calcareous grasslands between 1952–3 and 2001–3, which, together with an increase in Ellenberg N score, led to the suggestion that N deposition may be a factor in the decline. Van den Berg et al. (2011) found no relationship between species richness of calcareous grasslands and N deposition in a spatial analysis but temporal analysis indicated declines in species diversity over time (1990–3 to 2006–9) that were associated with N deposition. Temporal analysis from vegetation in North-western Germany failed to find changes in species richness related to N deposition (Diekmann et al., 2014). In neutral grasslands N additions in long-term experiments (Mountford et al., 1993 and Silvertown et al., 2006) suggest the potential for reductions in species richness.

Observations from gradients studies conducted in the UK and Europe (e.g. Payne et al., 2013, Stevens et al., 2011 and Van den Berg et al., 2011) and experimental N additions in various grassland types (e.g. Carroll et al., 2003, Mountford et al., 1993 and Phoenix et al., 2012) all show changing vascular plant, bryophyte or lichen species composition or above-ground biomass with increasing N deposition (summarised in Table 1). Studies have also identified particular species of vascular plants and lichens that are especially impacted by the addition of N (Henrys et al., 2011, Payne et al., 2013 and Stevens et al., 2012b).

Based on modelled results and literature review the following changes in semi-natural grasslands are projected for the year 2030:

- Declines in species richness seem likely in acid grasslands and possibly in other grassland types.
- An increase in the cover of grasses seems likely in all grassland types whereas forbs are the group most likely to decline in cover.
- An increase in the average Ellenberg N score is projected which reflects shifts towards more eutrophic vegetation.

- Some individual species of vascular plant are likely to decline in cover whereas other species more typical on nutrient rich conditions are likely to increase. The species changing will vary depending on grassland type.
- Some individual species of bryophyte are likely to show changes in abundance. The direction of change will depend on species identity.
- Terricolous lichens are likely to decrease in occurrence.

3.2. Heathland and bog

Results of this investigation suggest changes in species composition in the future under continued N deposition. Average Ellenberg N scores show a small increase between 1998 and 2020 and 2030 (Fig. 2) and species average HS is set to decline by 2030 as in other habitats. At high levels of N deposition some species see large reductions in HS compared to low deposition. Of 26 species with sufficient data for investigation 17 showed declines in HS but only four, *C. panicea* (−0.226), *Trichophorum cespitosum* (−0.215), *Calluna vulgaris* (−0.153) and *Erica tetralix* (−0.123) had reductions of over 10%. As with grasslands increases in HS were of a smaller magnitude with strongest increases seen for *Rumex acetosa* (0.039) and *Holcus lanatus* (0.032) (Fig. 5; Supplementary Table 1).

Nitrogen deposition has had a considerable impact on the vegetation of heathland communities in some parts of Europe, particularly The Netherlands, where cover of *Calluna vulgaris* and other dwarf shrubs has declined considerably and been replaced by grasses (Heil and Diemont, 1983). The process by which this change in vegetation cover has occurred is not simple and is described by Bobbink et al. (2010) as follows: N deposition commonly increases the productivity of dominant dwarf shrubs and much of the available N is retained in the soil promoting mineralisation. If the dwarf shrub canopy remains closed these species can remain the stronger competitor but if disturbance results in the opening of the canopy grasses become the stronger competitor as a result of higher light levels. Disturbance via heather beetle attacks, winter injury or drought are more likely under enhanced N deposition. Grass species that have increased in their cover at the expense of dwarf shrub species are *Molinia caerulea* and *Deschampsia flexuosa*. The devastating impact of N deposition on dwarf shrub vegetation in heathlands in The Netherlands has not been observed to date in the UK but without careful management there is the potential for these changes to occur at high levels of N deposition.

A number of gradient and long-term experimental N addition studies have investigated the impact of nitrogen addition on UK heathlands. Maskell et al. (2010) identified a significant negative association between N deposition and species richness of heathlands. Ellenberg N did not increase with increasing N deposition but Ellenberg R declined indicating soil acidification. Potential canopy height and grass:forb ratio increased whereas the number of forb species decreased. Field et al. (2014) found similar results reporting a reduction in species richness in both upland and lowland British heathlands with increasing N deposition as well as an increase in graminoid cover whilst Southon et al. (2013) also found litter C:N ratios and enzyme (phenol-oxidase and phosphomonoesterase) activities were also impacted. Other gradient studies have also demonstrated increases in litter N and reductions in species richness with N deposition (Edmondson et al., 2010, Payne et al., 2014 and

Caporn et al., 2014). Armitage et al. (2012) investigated *Racomitrium lanuginosum* condition in 36 heathland sites across Europe showing increased growth rates but reduced moss mat depth and cover. Experimental N additions in a montane heath also found similar results (Pearce and van der Wal, 2002 and Pearce et al., 2003).

The UK hosts some of the world's longest running heathland N addition experiments including Ruabon upland heath and Thursley lowland heath which were both established in 1989. Further long term experiments in the UK are Budworth lowland heathland and Culardoch low alpine heath. These experiments are summarised in Phoenix et al. (2012). Results across these experiments consistently show no change in higher plant richness but declines in lichen abundance, an increase in flowering and an increase in secondary stress. Productivity was increased at all sites but declined again at higher levels at Ruabon (Phoenix et al., 2012).

Henrys et al. (2011) used national vegetation surveillance data recording presence of vascular plant species between 1987 and 1999 and between 2003 and 2004 to examine the occurrence of individual habitat specialist species in relation to N deposition. In lowland heathlands *Viola canina* showed a negative relationship with N deposition whilst *Plantanthera bifolia* had a positive relationship. In upland heathlands *Arctostaphylos uva-ursi* and *Vaccinium vitis-idaea* showed negative relationships with N deposition. They also found that Ellenberg N values increased with increasing N deposition. Stevens et al. (2012b) took the same approach to investigate the occurrence of terricolous lichens. 26 taxa were investigated for heathland with nine showing significant negative relationships with N deposition. Many of the species reached a very low probability of presence by N deposition rates of 20 kg N ha⁻¹ yr⁻¹. Experimental investigation of N concentration and deposition effects on five terricolous lichen species also showed a very high sensitivity (Britton and Fisher, 2010).

Ombrotrophic bogs rely on atmospheric deposition for nutrient inputs and consequently even small increases in N deposition have the potential to bring about changes in vegetation. There are fewer long-term studies in bog habitats than in heathland but the Whim Bog experiment provides realistic long-term N addition. The experiment was established in 2002 on an ombrotrophic bog (UK NVC community M19). N is added in rainwater sprayed as fine droplets using an automated system. Dry deposition of NH₃ is provided on a transect with deposition ranging from 4 to 70 kg N ha⁻¹ yr⁻¹. In the dry deposition gradient N treatments have resulted in large changes in species composition with an expansion of *Eriophorum vaginatum*, *Vaccinium myrtillus* and *Empetrum nigrum*, and a decline in *Calluna vulgaris* and *Sphagnum capillifolium*. These changes were not observed in the wet deposition treatment (Phoenix et al., 2012 and Sheppard et al., 2011). *Sphagnum* mosses are very important in bog communities, not only as a dominant genus but also because they help maintain hydrological regimes and form peat. Some species of *Sphagnum* moss have been shown to have reduced growth under N addition (Limpens and Berendse, 2003). In a modelling exercise Granath et al. (2014) predicted reduced production and abundance of *Sphagnum* under future N deposition and climate change.

In a survey of 29 bog sites on a gradient of N deposition Field et al. (2014) found reduced lichen and forb species richness and increased graminoid cover at high deposition rates. Other investigations in the Netherlands have suggested that N deposition may be partly responsible for invasion of grass

and trees to bog habitats although hydrology is likely to play an important role in any vegetation change (Tomassen et al., 2003).

Based on modelled results and literature review the following changes in heathland and bog vegetation are projected for the year 2030:

- A reduction in species richness seems likely in both heathlands and bogs.
- A reduction in the cover of dwarf shrubs including *Calluna vulgaris* and *Erica* spp seems likely in both heathland and bogs. Grass cover, particularly *Molinia caerulea*, *Holcus lanatus* and *Deschampsia flexuosa*, is likely to increase.
- An increase in the average Ellenberg N score is projected which reflects shifts towards more eutrophic vegetation.
- Some individual species of vascular plant are likely to decline in cover. The species changing will vary depending on whether the habitat is a heathland or bog.
- Some species of *Spagnum* moss are likely to decline in productivity.
- Terricolous lichens are likely to decrease in occurrence.

3.3. Deciduous woodland

In deciduous woodland our models predict that Ellenberg N values will increase slightly (Fig. 2). As a consequence of this change in nutrient status the model predicts that there will be changes in HS of key species. In areas of low deposition these changes are minimal (Fig. 3). There are however, several species that show a greater degree of change in HS, most of these species are those typical of low nutrient status habitats and would only be expected to be found in a restricted number of woodland types. The species most negatively impacted by high levels of N deposition (greater than the median cumulative N point which was 1817.6 kg N ha⁻¹) is *Calluna vulgaris* (for the year 2020 high deposition HS for *Calluna vulgaris* is 0.173). Of the twelve other species examined (Supplementary Table 1) nine showed a negative change in HS. *Juncus effusus* was the only species that showed a positive response but the magnitude of this change was very small (0.005).

Studies of the impacts of N deposition on vegetation have mainly focussed on woodland ground flora and this is where we will focus in this investigation. The importance of woodland management and the influence it has on the canopy and light levels make it difficult to predict responses to N deposition in woodlands, this may act to mask effects of N deposition in a closed canopy where eutrophic species cannot invade due to low light levels. Studies throughout Europe have shown evidence for changes in biomass (Nellemann and Thomsen, 2001) and ground flora composition (Pitcairn et al., 1998). Woodlands on nutrient poor soils are most likely to be sensitive to N deposition.

There have been relatively few N addition experimental studies in woodlands that have focussed on impacts of ground flora and even fewer in the UK or in habitats analogous to those found in the UK. There is more evidence from national and local monitoring and gradient studies. A national

woodland survey in 2001, repeating a similar one in 1971, found no overall shift in species towards more fertile/eutrophic assemblages and no change in mean Ellenberg N score. High levels of intensive land use surrounding woods were associated with increases in Ellenberg N scores (Kirby et al., 2005). In The Netherlands changes in vegetation composition and increases in nitrophilic species have been observed. Brunet et al. (1998) reported an increase in nitrophilous species and increases in grass cover, especially of *Deschampsia flexuosa*. In Sweden, an increase in nitrophilous species at low pH and high N deposition has been reported and increases in Ellenberg N were also found (Diekmann and Falkengren-Grerup, 1998). Using a gradient away from an ammonia point source Pitcairn et al. (1998) identified a number of vegetation changes related to ammonia concentrations. Nitrophilous species such as *Deschampsia flexuosa*, *Holcus lanatus*, *Rubus idaeus* and *Urtica dioica* were found at higher levels of cover close to the source than further away. More N-sensitive species such as *Oxalis acetosella*, *Galium odoratum*, and ferns were scarce close to the source. In a survey of Atlantic oak woodlands in the UK Mitchell et al. (2005) found that epiphytic species of lichen and bryophytes were related to ammonium concentration in stemflow. Bryophytes *Isoetecium myosuroides* and *Frullania tamarisci* were indicators of low N stemflow whereas other species such as *Hypnum andoi*, *Hypogymnia physodes* and *Parmelia saxatilis* were more tolerant of higher N stemflow.

Based on modelled results and literature review the following changes in deciduous woodlands are projected for the year 2030:

- An increase in grass cover seems likely in woodlands where species are adapted to a low nutrient status.
- An increase in the average Ellenberg N score is projected which reflects shifts towards more eutrophic vegetation.
- Species composition is likely to change. It seems likely that there will be increases in the cover and occurrence of more nitrophilic vascular plant species such as *Deschampsia flexuosa*, *Holcus lanatus*, *R. idaeus* and *Urtica dioica*. Some other species such as *Calluna vulgaris* and *O. acetosella* are likely to decline.
- Epiphytic bryophyte and lichen communities are likely to change in species composition.
- Epiphytic lichens are likely to be reduced in occurrence.

4. Caveats

It is important to recognise the limitations of our modelling study. In particular, all of our modelling is based on an assumption that recovery from N deposition impacts is not possible. While this is clearly a simplification we believe it is currently the best option due to the limited available data on recovery of vegetation from reduced deposition. Remedying this data-gap is critical to more accurate predictions in the future. It should also be noted that Ellenberg N values underlie our models and this index has well-known limitations as a representation of N deposition impacts. We

were also not able to model responses to changes in management which may occur. Despite these acknowledged limitations we believe our conclusions are reasonably robust as they are based upon both modelling and an assessment of the very extensive air pollution effects literature.

5. Conclusions

Nitrogen deposition has many impacts on the biodiversity of (semi-)natural terrestrial ecosystems encompassing loss of species and changed community composition at multiple trophic levels. Review of literature and analysis of species niche requirements suggests that HS is likely to decline for a number of species. A number of habitats are likely to see an increase in graminoids and eutrophic species whilst species less able to compete well in nutrient rich situations and some lichen species are likely to decline. Evidence from gradient studies in a range of habitats (Field et al., 2014, Maskell et al., 2010 and Stevens et al., 2010) suggest that areas that currently experience low levels of N deposition are likely to be most sensitive to increases in deposition. The mechanisms for changes are likely to be related to soil mediated effects of eutrophication and acidification and associated changes in soil chemistry. It is likely that mechanisms will vary between habitats, and be influenced by factors such as soil type and management. Reducing N emissions and deposition is the only way that impacts of N deposition can be reduced at a national scale; this should be a priority for national conservation agencies and regulatory bodies to protect biodiversity across the UK.

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Tables

Table 1. Summary of vegetation (diversity, productivity and species composition) responses to N deposition in published gradient studies and N addition experiments in UK grasslands.

Grassland type	Study details	Vegetation responses to N deposition	References
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Gradient studies

Acid grassland (NVC U4)	Great Britain, 2002-2003, ambient deposition gradient, 68 sites, stratified random sampling to cover range of N deposition, five 2 x 2 m quadrats randomly located within 1 ha sampling area. N deposition range 5-35 kg N ha ⁻¹ yr ⁻¹ . European survey extended analysis to other		
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European countries. Reduced species richness, reduced richness and cover of forbs, increased grass:forb ratio, changes in species composition, Ellenberg R reduced. (Payne et al., 2013; Stevens et al., 2006; Stevens et al., 2004; Stevens et al., 2010; Stevens et al., 2011)

Acid grassland (NVC U1–9), Calcareous grassland

(CG2, 3, 4, 6, 8, 10, 11), Mesotrophic grassland (MG6

and MG7) Countryside survey of Great Britain, 1998, acid grasslands 895 plots; calcareous grasslands 94 plots; mesotrophic grasslands 1342 plots, stratified random selection of 1 km squares and stratified random sampling of 2 x 2 m plots within that. Sites classified to grassland type using NVC descriptions. N deposition range 5-40 kg N ha⁻¹ yr⁻¹. Acid grassland – reduced species richness, reduced Ellenberg R (increased acidity), reduced forb richness, increased grass:forb ratio

Calcareous grassland – no significant relationship with N deposition, canopy height increased, grass:forb ratio increased, Ellenberg N increased.

Mesotrophic grassland – very weak negative relationship with N deposition, Slight increase in Ellenberg N (Maskell et al., 2010)

Chalk grassland South and East England, 2001-3 resurvey of plots collected in 1952-3, original sites selected to cover a range of slopes and aspects, 92 plots, 50 m² plots with 20 10 x 10 cm random sampling points, temporal analysis but N deposition not specifically included as a variable. N deposition range 15-34 kg N ha⁻¹ yr⁻¹. Temporal changes identified but not specifically related to N deposition: species richness declined, increase in competitive grasses and loss of stress-tolerant calcareous grassland species, Ellenberg N increased. (Bennie et al., 2006)

Calcareous grassland England and Scotland, 2009-9 resurvey of plots collected in 1990-3, original sites selected to provide geographical range, 35 plots, permanently marked plots 144 m² with 36 50 x 50 cm quadrats, temporal and spatial analysis. N deposition range 7-41 kg N ha⁻¹ yr⁻¹.

Spatial analysis - no relationship between N deposition and species richness, no scarce or rare species above 25 kg N ha⁻¹ yr⁻¹. Temporal analysis – declines in species diversity and evenness (Van den Berg et al., 2011)

Dune grassland Great Britain, 2001, dune systems from mobile dunes to dune grassland, eight survey points along transects, two 2 x 2 m quadrats per survey point, 25 x 25 cm area clipped for biomass. N deposition range 7-30 kg N ha⁻¹ yr⁻¹. Species richness decreased, biomass increased and the vegetation N pool increased. (Jones et al., 2004)

Dune grassland (Eunis code B1.4) Great Britain, 2009, 24 plots, stratified random sampling to cover range of climate and N deposition, five 2 x 2 m quadrats randomly located within 1 ha sampling area. N deposition range 5-17 kg N ha⁻¹ yr⁻¹. Reduced species richness, bryophyte, forb, graminoid and lichen diversity. Increased cover of graminoids. (Field et al., in press 2014)

Acid grassland (NVC U1–9), Calcareous grassland

(CG2, 3, 4, 6, 8, 10, 11) Great Britain, since 1960, national surveillance data from British Lichen Society records for presence of all lichen taxa growing within 10 km² hectads. N deposition range 5-

35 kg N ha⁻¹ yr⁻¹. Changes in the occurrence of individual terricolous lichen species. Most species investigated showed a negative response. (Stevens et al., 2012b)

Acid grassland (NVC U1–9), Calcareous grassland

(CG2, 3, 4, 6, 8, 10, 11) Great Britain, 1987-99, national surveillance data from The Vascular Plant Database for presence of vascular plant species in 10 km² hectads; and 2003-4, The Botanical Society of the British Isles (BSBI) Local Change Survey data for presence of vascular plant species in 811 2×2 km tetrads located within a regular

grid of 10 km² hectads. Changes in the occurrence of individual species, increases in Ellenberg N scores. (Henrys et al., 2011)

Acid grassland (Violion

Caninae) Great Britain (data from Netherlands and Germany also presented), published vegetation data 1960-2003, 541 plots 0.25-4 m², cumulative N deposition range 130-868 in year 2000 eq ha⁻¹ yr⁻¹. Changes in species composition, increase in Ellenberg N, vascular plant richness declined, number of dicots declined, number of bryophytes declined. (Duprè et al., 2010)

Experiments

Acid grassland (NVC U4) Wardlow Hay Cop, Peak District, initiated 1990, 0, 35, 70, 140 kg N ha⁻¹ yr⁻¹ applied monthly as a fine spray. Background deposition 34 kg N ha⁻¹ yr⁻¹. Decline in forb cover and increase in grass cover, large decline in bryophyte cover, productivity increased. (Arroniz-Crespo et al., 2008; Carroll et al., 2003; Morecroft et al., 1994; Phoenix et al., 2012)

Calcareous grassland (NVC CG2) Wardlow Hay Cop, Peak District, initiated 1990, 0, 35, 70, 140 kg N ha⁻¹ yr⁻¹ NH₄NO₃ applied monthly as a fine spray. Background deposition 34 kg N ha⁻¹ yr⁻¹. Decline in forb cover and increase in grass cover, decline in bryophyte cover at highest level, productivity increased. (Arroniz-Crespo et al., 2008; Carroll et al., 2003; Morecroft et al., 1994; Phoenix et al., 2012)

Fixed dune grassland (NVC SD8) Newborough, North Wales, initiated 2003, 0, 10, 20 kg N ha⁻¹ yr⁻¹ NaNO₃ and (NH₄)₂SO₄ applied fortnightly using a watering can. Background deposition 17 kg N ha⁻¹ yr⁻¹. Bryophyte abundance increased, productivity increased. (Phoenix et al., 2012; Plassmann et al., 2010)

Acid grassland (NVC U4) Pwllpeiran, North Wales, initiated 2003, 0, 25, 50, 100, 200 kg N ha⁻¹ yr⁻¹ NH₄NO₃ applied twice per year. Background deposition 21 kg N ha⁻¹ yr⁻¹. *Vaccinium myrtillus* has declined, *Carex pilulifera* increased under a light grazing regime and the oxidized (not reduced) N treatment. (Phoenix et al., 2012)

Neutral grassland (NVC MG5) Tatham Moor, Somerset, ran 1986-1993, 0, 7.5, 15 kg N ha⁻¹ yr⁻¹ NH₄NO₃ applied monthly using a watering can, grazing treatment. Background deposition 11 kg N ha⁻¹ yr⁻¹. Species richness declined, competitive grass species increased, seed bank changed to favour competitive species. (Mountford et al., 1996; Mountford et al., 1993)

Acid grassland (NVC U4)Trefor, North Wales (replicated experimental sites in Norway and France), initiated 2007, 0, 75, 70 kg N ha⁻¹ yr⁻¹ NH₄NO₃ and 70 kg N ha⁻¹ yr⁻¹ NaNO₃ and NH₄Cl applied eight times per year. Background deposition 9 kg N ha⁻¹ yr⁻¹. Non-significant increase in biomass. (Dorland et al., 2013)

Neutral grassland (NVC MG5) Park grass experiment, Harpenden, initiated 1856, N, P, K and manure addition in various combinations, N only plots are 48 kg N ha⁻¹ yr⁻¹ NaNO₃ applied annually. Background deposition 35 kg N ha⁻¹ yr⁻¹. Increase in grass cover, species richness reduced. (Silvertown et al., 2006)

Figure legends

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Figure 4. Projected habitat suitability scores for *Carex panicea*, *Lotus corniculatus*, *Plantago lanceolata* and *Urtica dioica* in grassland calculated using the MultiMOVE model against projected cumulative N deposition (kg N ha⁻¹) for 1998, 2020 and 2030.

Figure 5. Projected habitat suitability scores for *Tricophorum cespitosum*, *Calluna vulgaris*, *Erica tetralix* and *Rumex acetosa* in heathland and bog woodland calculated using the MultiMOVE model against projected cumulative N deposition (kg N ha⁻¹) for 1998, 2020 and 2030.

Tables

Table 1. Summary of vegetation (diversity, productivity and species composition) responses to N deposition in published gradient studies and N addition experiments in UK grasslands.

Grassland type	Study details	Vegetation responses to N deposition	References
Gradient studies			
Acid grassland (NVC U4)	Great Britain, 2002-2003, ambient deposition gradient, 68 sites, stratified random sampling to cover range of N deposition, five 2 x 2 m quadrats randomly located within 1 ha sampling area. N deposition range 5-35 kg N ha ⁻¹ yr ⁻¹ . European survey extended analysis to other European countries.	Reduced species richness, reduced richness and cover of forbs, increased grass:forb ratio, changes in species composition, Ellenberg R reduced.	(Payne et al., 2013; Stevens et al., 2006; Stevens et al., 2004; Stevens et al., 2010; Stevens et al., 2011)
Acid grassland (NVC U1–9), Calcareous grassland (CG2, 3, 4, 6, 8, 10, 11), Mesotrophic grassland (MG6 and MG7)	Countryside survey of Great Britain, 1998, acid grasslands 895 plots; calcareous grasslands 94 plots; mesotrophic grasslands 1342 plots, stratified random selection of 1 km squares and stratified random sampling of 2 x 2 m plots within that. Sites classified to grassland type using NVC descriptions. N deposition range 5-40 kg N ha ⁻¹ yr ⁻¹ .	Acid grassland – reduced species richness, reduced Ellenberg R (increased acidity), reduced forb richness, increased grass:forb ratio Calcareous grassland – no significant relationship with N deposition, canopy height increased, grass:forb ratio increased, Ellenberg N increased. Mesotrophic grassland – very weak negative relationship with N deposition, Slight increase in Ellenberg N	(Maskell et al., 2010)
Chalk grassland	South and East England, 2001-3 resurvey of plots collected in 1952-3, original sites selected to cover a range of slopes and aspects, 92 plots, 50 m ² plots with 20 10 x 10 cm random sampling points, temporal analysis but N deposition not specifically included as a variable. N deposition range 15-34 kg N ha ⁻¹ yr ⁻¹ .	Temporal changes identified but not specifically related to N deposition: species richness declined, increase in competitive grasses and loss of stress-tolerant calcareous grassland species, Ellenberg N increased.	(Bennie et al., 2006)
Calcareous grassland	England and Scotland, 2009-9 resurvey of plots collected in 1990-3, original sites selected to provide geographical range, 35	Spatial analysis - no relationship between N deposition and species richness, no scarce or rare species above 25 kg N ha ⁻¹	(Van den Berg et al., 2011)

	plots, permanently marked plots 144 m ² with 36 50 x 50 cm quadrats, temporal and spatial analysis. N deposition range 7-41 kg N ha ⁻¹ yr ⁻¹ .	yr ⁻¹ . Temporal analysis – declines in species diversity and evenness	
Dune grassland	Great Britain, 2001, dune systems from mobile dunes to dune grassland, eight survey points along transects, two 2 x 2 m quadrats per survey point, 25 x 25 cm area clipped for biomass. N deposition range 7-30 kg N ha ⁻¹ yr ⁻¹ .	Species richness decreased, biomass increased and the vegetation N pool increased.	(Jones et al., 2004)
Dune grassland (Eunis code B1.4)	Great Britain, 2009, 24 plots, stratified random sampling to cover range of climate and N deposition, five 2 x 2 m quadrats randomly located within 1 ha sampling area. N deposition range 5-17 kg N ha ⁻¹ yr ⁻¹ .	Reduced species richness, bryophyte, forb, graminoid and lichen diversity. Increased cover of graminoids.	(Field et al., 2014)
Acid grassland (NVC U1–9), Calcareous grassland (CG2, 3, 4, 6, 8, 10, 11)	Great Britain, since 1960, national surveillance data from British Lichen Society records for presence of all lichen taxa growing within 10 km ² hectads. N deposition range 5-35 kg N ha ⁻¹ yr ⁻¹ .	Changes in the occurrence of individual terricolous lichen species. Most species investigated showed a negative response.	(Stevens et al., 2012b)
Acid grassland (NVC U1–9), Calcareous grassland (CG2, 3, 4, 6, 8, 10, 11)	Great Britain, 1987-99, national surveillance data from The Vascular Plant Database for presence of vascular plant species in 10 km ² hectads; and 2003-4, The Botanical Society of the British Isles (BSBI) Local Change Survey data for presence of vascular plant species in 811 2x2 km tetrads located within a regular grid of 10 km ² hectads.	Changes in the occurrence of individual species, increases in Ellenberg N scores.	(Henry et al., 2011)
Acid grassland (<i>Violion Caninae</i>)	Great Britain (data from Netherlands and Germany also presented), published vegetation data 1960-2003, 541 plots 0.25-4 m ² , cumulative N deposition range 130-868 in year 2000 eq ha ⁻¹ yr ⁻¹ .	Changes in species composition, increase in Ellenberg N, vascular plant richness declined, number of dicots declined, number of bryophytes declined.	(Duprè et al., 2010)
Experiments			
Acid grassland (NVC U4)	Wardlow Hay Cop, Peak District, initiated 1990, 0, 35, 70, 140 kg N ha ⁻¹ yr ⁻¹ applied monthly as a	Decline in forb cover and increase in grass cover, large decline in bryophyte cover,	(Arroniz-Crespo et al., 2008; Carroll et al.,

	fine spray. Background deposition 34 kg N ha ⁻¹ yr ⁻¹ .	productivity increased.	2003; Morecroft et al., 1994; Phoenix et al., 2012)
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Neutral grassland (NVC MG5)	Park grass experiment, Harpenden, initiated 1856, N, P, K and manure addition in various combinations, N only plots are 48 kg N ha ⁻¹ yr ⁻¹ NaNO ₃ applied annually. Background deposition 35 kg N ha ⁻¹ yr ⁻¹ .	Increase in grass cover, species richness reduced.	(Silvertown et al., 2006)

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Figure 1.

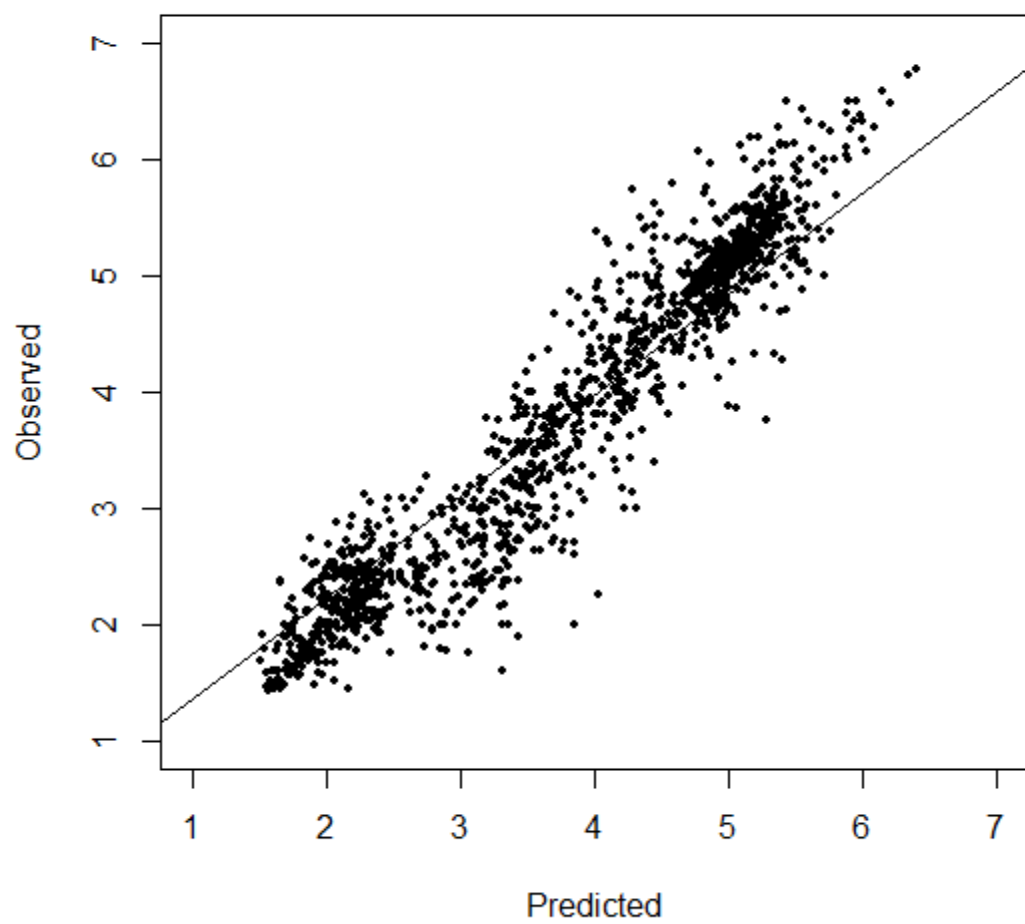


Figure 2.

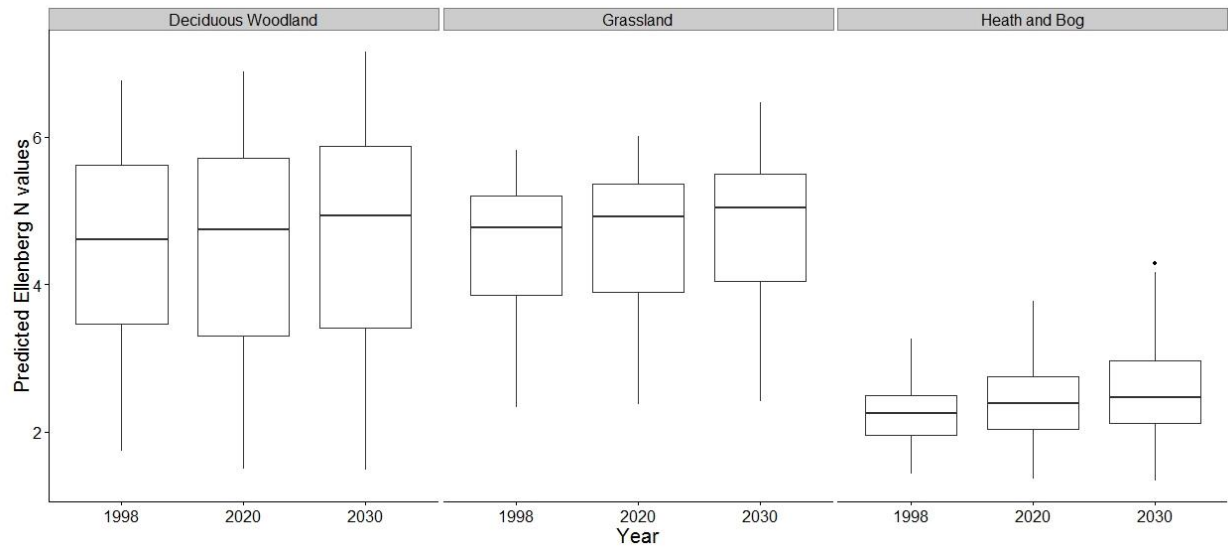


Figure 3

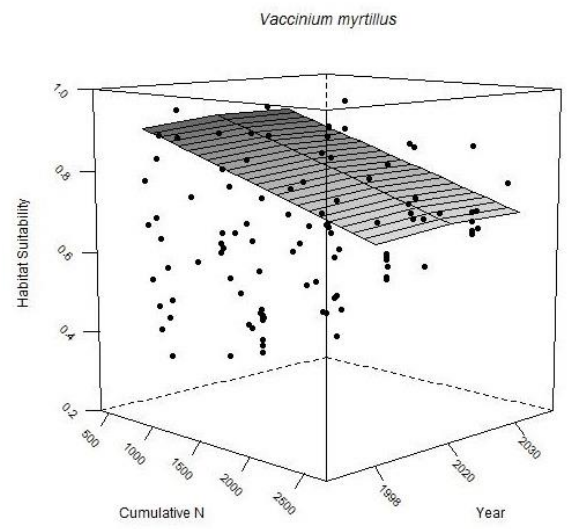
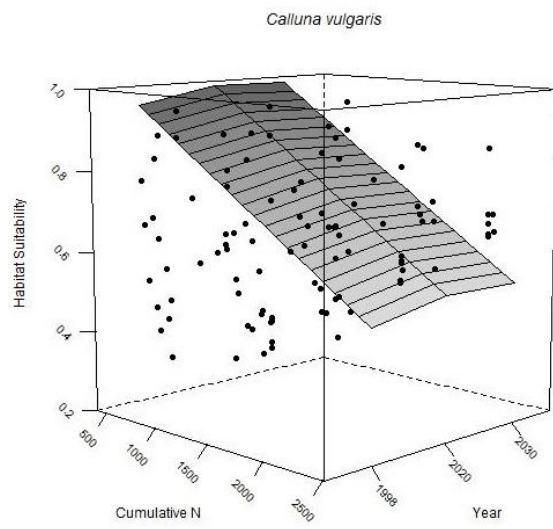


Figure 4

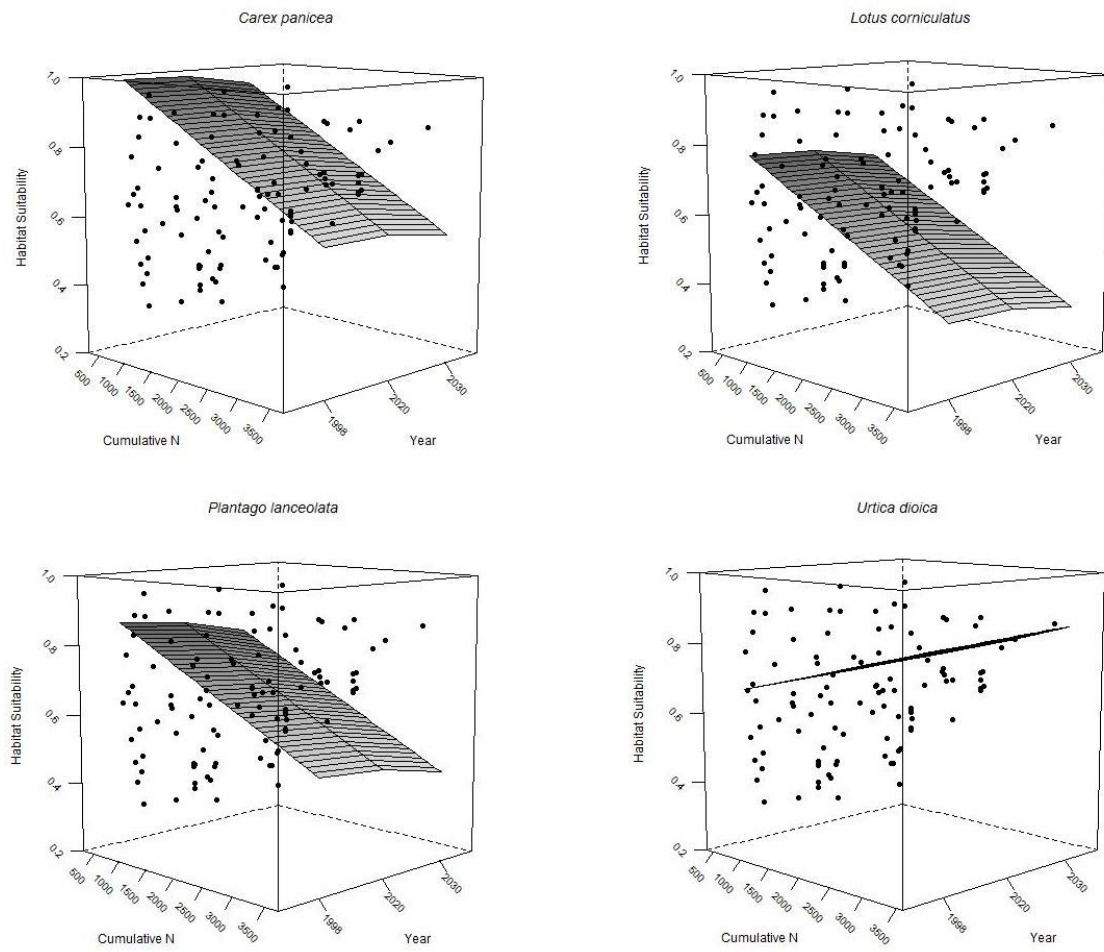
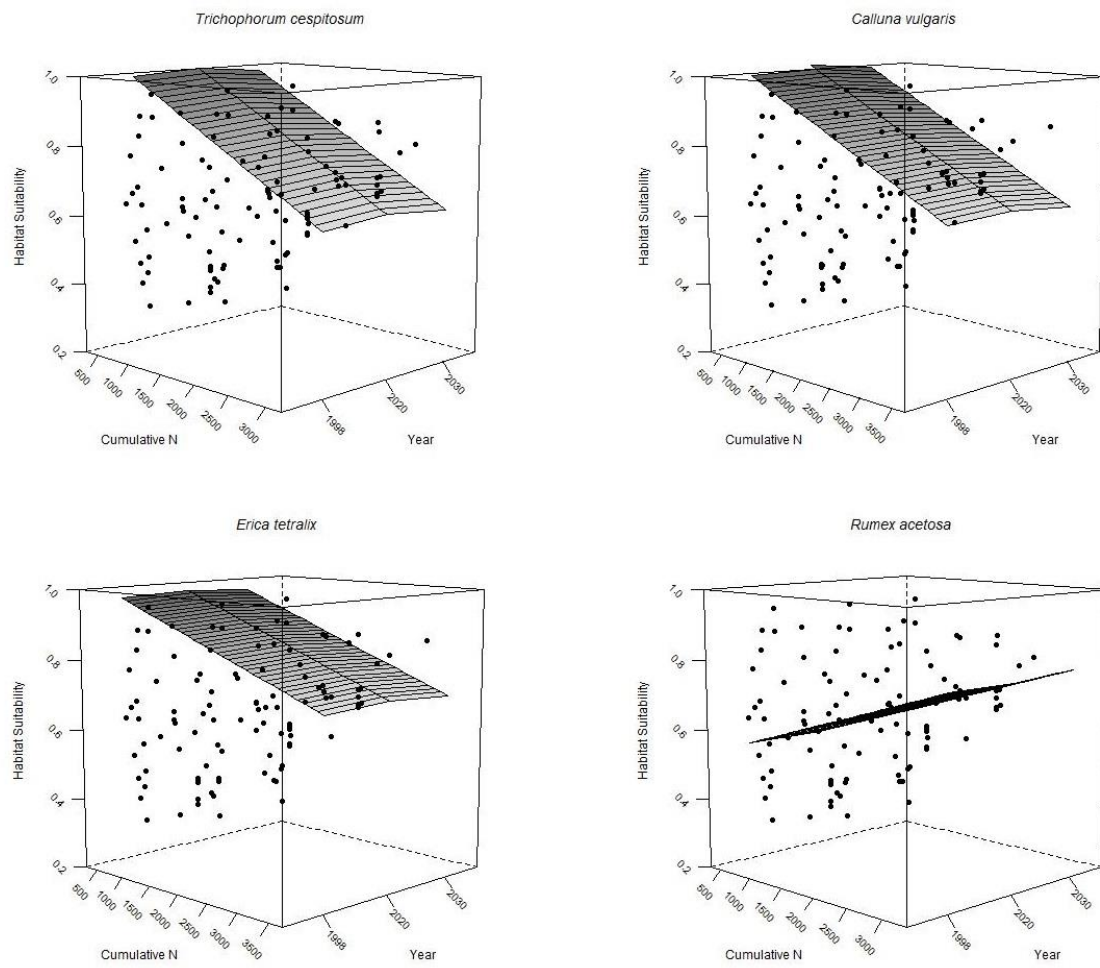


Figure 5



Supplementary Table 1. Change in habitat suitability (HS) between 1998 and 2030 for individual species in broadleaved woodland, grassland and heathland and bog calculated using the the MultiMOVE model with predicted cumulative N deposition. Scores are presented for high and low deposition (based on deposition above and below the median).

Species	HS change high N deposition	HS change low N deposition
Deciduous Woodland		
<i>Calluna vulgaris</i>	-0.173	-0.021
<i>Festuca rubra</i> agg.	-0.116	-0.017
<i>Potentilla erecta</i>	-0.110	-0.015
<i>Anthoxanthum odoratum</i>	-0.058	-0.007
<i>Vaccinium myrtillus</i>	-0.031	-0.001
<i>Holcus lanatus</i>	-0.024	-0.002
<i>Agrostis capillaris</i>	-0.017	0.001
<i>Galium saxatile</i>	-0.012	-0.001
<i>Deschampsia flexuosa</i>	-0.008	-0.001
<i>Pteridium aquilinum</i>	-0.006	0.000
<i>Agrostis stolonifera</i>	-0.004	0.000
<i>Juncus effusus</i>	0.005	0.004
Grassland		
<i>Carex panicea</i>	-0.234	-0.017
<i>Calluna vulgaris</i>	-0.190	-0.018
<i>Lotus corniculatus</i>	-0.172	-0.021
<i>Plantago lanceolata</i>	-0.164	-0.032
<i>Eriophorum angustifolium</i>	-0.122	-0.013
<i>Festuca rubra</i> agg.	-0.127	-0.019
<i>Eriophorum vaginatum</i>	-0.113	-0.013
<i>Potentilla erecta</i>	-0.096	-0.012
<i>Molinia caerulea</i>	-0.085	-0.006
<i>Prunella vulgaris</i>	-0.105	-0.031
<i>Juncus squarrosus</i>	-0.075	-0.005
<i>Nardus stricta</i>	-0.070	-0.009
<i>Festuca ovina</i> agg.	-0.075	-0.015
<i>Achillea millefolium</i>	-0.065	-0.010
<i>Leontodon autumnalis</i>	-0.056	-0.011
<i>Ranunculus acris</i>	-0.048	-0.008
<i>Anthoxanthum odoratum</i>	-0.046	-0.007
<i>Senecio jacobaea</i>	-0.048	-0.012
<i>Cirsium palustre</i>	-0.034	-0.001
<i>Vaccinium myrtillus</i>	-0.036	-0.006
<i>Veronica chamaedrys</i>	-0.037	-0.013
<i>Dactylis glomerata</i>	-0.037	-0.018

Carex echinata	-0.020	-0.001
Carex nigra	-0.016	0.002
Rumex acetosa	-0.025	-0.007
Cynosurus cristatus	-0.025	-0.008
Agrostis canina sens.lat.	-0.015	0.000
Agrostis capillaris	-0.016	-0.002
Holcus lanatus	-0.016	-0.004
Deschampsia cespitosa	-0.007	0.006
Deschampsia flexuosa	-0.007	-0.001
Cirsium arvense	-0.007	-0.003
Bellis perennis	-0.002	0.001
Agrostis stolonifera	-0.004	0.000
Pteridium aquilinum	-0.002	0.000
Taraxacum agg.	-0.003	-0.001
Cirsium vulgare	-0.002	-0.001
Cerastium fontanum	0.000	0.000
Galium saxatile	-0.003	-0.003
Trifolium repens	0.000	-0.001
Rumex acetosella	0.002	0.000
Poa pratensis sens.lat.	0.007	0.001
Lolium perenne	0.013	0.008
Juncus effusus	0.011	0.005
Ranunculus repens	0.011	0.002
Holcus mollis	0.039	0.025
Poa annua	0.031	0.005
Stellaria media	0.046	0.019
Poa trivialis	0.034	0.005
Urtica dioica	0.061	0.025
Heath and Bog		
Carex panicea	-0.239	-0.013
Trichophorum cespitosum	-0.234	-0.019
Calluna vulgaris	-0.168	-0.015
Erica tetralix	-0.133	-0.010
Eriophorum angustifolium	-0.101	-0.011
Festuca rubra agg.	-0.093	-0.007
Eriophorum vaginatum	-0.095	-0.009
Potentilla erecta	-0.081	-0.008
Juncus squarrosus	-0.072	-0.005
Molinia caerulea	-0.065	-0.005
Nardus stricta	-0.057	-0.008
Festuca ovina agg.	-0.047	-0.009
Vaccinium myrtillus	-0.031	-0.005
Trifolium repens	-0.012	-0.003
Deschampsia flexuosa	-0.008	-0.001
Anthoxanthum odoratum	-0.009	-0.002
Agrostis canina sens.lat.	0.000	0.003

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